OLD AGE IN BRACHIOPODA — A PRELIMINARY STUDY

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THE following paper was prepared as the result of studies pursued at Harvard University under the direction of Professor R. T. Jackson, to whose oversight and suggestive criticisms the writer is indebted. Thanks are also due Mr. R. H. Willcomb of Ipswich, Mass., for his kindness in taking the photographs.

In this study we have made use of the fine collection of the Student Paleontological Department of Harvard University, the collections of the Boston Society of Natural History, and those of the Massachusetts Institute of Technology. Unless otherwise stated, the specimens referred to are in the Student Paleontological Laboratory at Harvard University. Those from the Massachusetts Institute of Technology are either still in that institution or have since been transferred to the Boston Society of Natural History.

This paper aims to summarize the principal characters which accompany old age in brachiopods, to illustrate them with some typical examples, and to present a few suggestions as to their origin and meaning.

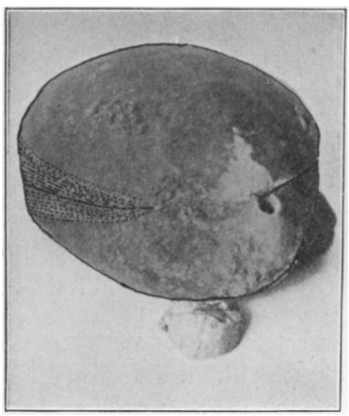
Following the present usage, we employ the terms, nepionic for the larval or postembryonic stage of an animal's individual development; neanic for the immature or adolescent; ephebic for the mature or adult; and gerontic for the senile or old. Each one of these is further subdivided into three substages by the prefixes, ana-, meta-, and para-, denoting the beginning of a given stage, its culmination, and its decline (Hyatt, '94, pp. 390–397; '93, pp. 93–108).

SENILE CHARACTERS

Senility is expressed in the shell by one or more, frequently all, of the following characters:—

1. *Lamellosity of Growth Lines.*— The concentric growth lines become more closely spaced and lamellose, with a tendency to pile up at the lateral and anterior borders of the shell.

Examples: a pedicle valve of *Laqueus californicus* Koch, No.



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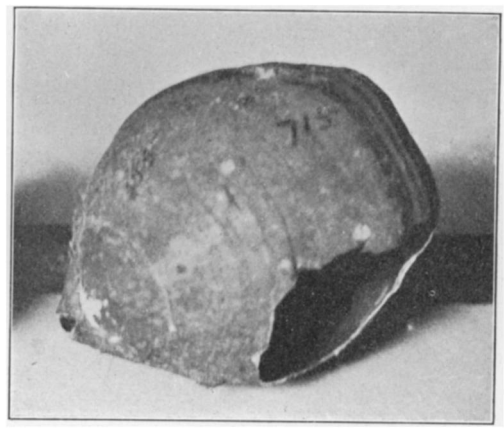

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FIG. 1.— A senile individual of *Laqueus californicus* Koch from Catalina Island, California. Old age is indicated by the lamellosity of the concentric growth lines on the gerontic portion of the shell and by the change there in the angle of curvature. The resorption of the umbo by the pedicle is likewise shown. No. 715, Harvard.

FIG. 1a.— A different view of the individual seen in Fig. 1, showing resorption of the umbo and of the deltidial plates by the pedicle.

715, up to and including its mature growth, a length of 40 mm., has only one or two strongly marked growth lines, while on its

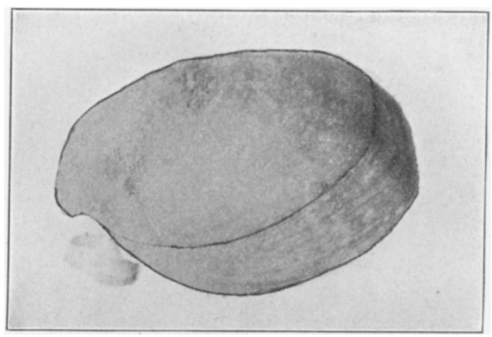

FIG. 2.— A side view of the individual seen in Fig. 1, showing anteriorly the change in the angle of curvature.

gerontic portion there are at least eight in a length of but 10 mm. (Figs. 1 and 2.)

A specimen of *Atrypa spinosa* Hall, No. 499, has in its mature or ephebic stage a length antero-posteriorly of 30 mm. or of 36 mm. measured on the curve of the pedicle valve. In succeeding growth originated a change in the angle of curvature at the anterior portion of the shell, indicating old age (see below). From the umbo up to and including the mature portion of the shell there are 24 well marked growth lines about equidistant; on the gerontic or deflected portion there are nine growth lines in a space of but 4.5 mm. Thus in old age the growth lines become crowded, as one occurs in every 0.5 mm., while in the previous growth one occurred in only every 1.5 mm. The piling up of the growth lines was caused by their continued production unac-

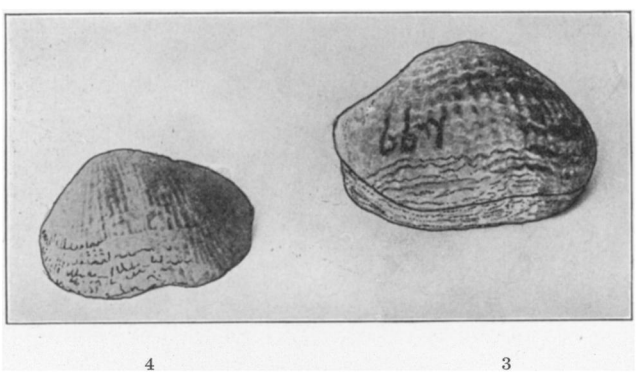

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FIG. 3.— A very large senile individual of *Atrypa spinosa* Hall from the Hamilton of Eighteen Mile Creek, New York, showing the change in the angle of curvature, the groove at the junction of the valves, and the lamellose condition of the growth lines upon the gerontic portion of the shell. No. 499, Harvard.

FIG. 4.— A fully mature individual of *Atrypa spinosa* Hall, on which none of the above gerontic features appear.

companied by any considerable growth of the shell in the anterior direction (Fig. 3).

A Lower Helderberg specimen of *Atrypa reticularis* (Linné), No. 641, shows 12 growth lines on the gerontic portion in less than 5 mm. This is after the abrupt deflection while the preceding portion of about 21 mm. in length also had only 12.

2. *Change in the Angle of Curvature.—This often results in a groove at the junction of the two valves.* An abrupt change in

direction occurs at the lateral and anterior borders of the shell so as to produce maximum growth almost or completely at right angles to the plane of separation of the valves. This change is frequently so great as to produce a reëntrant groove of greater or less depth at the junction of the valves, at the lateral and anterior portions of the shell. The groove results from the failure of each successive growth line to build out as far as the preceding one, and thus results in bending in the edges of the valves so that they meet in a depression.

Examples: in a pedicle valve of *Athyris spiriferoides* (Eaton), No. 498, the first lamellose growth lines appear after the shell has attained a length of 22 mm. and a width of 26 mm. At this period in growth the shell not only ceased to increase in width at the cardinal angles but actually decreased and so produced a groove

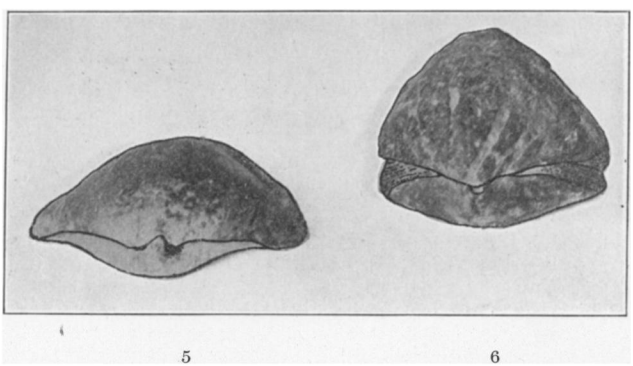

FIG. 5.— *Athyris spiriferoides* (Eaton). A mature individual from the Hamilton group of Eighteen Mile Creek, New York.

FIG. 6.— A senile individual of *Athyris spiriferoides* (Eaton) from the Hamilton of Eighteen Mile Creek, New York. Gerontism is well shown here in the change in the angle of curvature and the conspicuous groove at the junction of the valves. No. 498, Harvard.

1 mm. in depth (Fig. 6). The change in the angle of curvature took place at the anterior portion of the valve later than at the cardinal angles.

In a specimen of *Laqueus californicus*, No. 715, measuring 45 mm. in length by 35 mm. in width, the change in the angle of curvature in old age at the sides of the shell is about 45°, and at the anterior portion is much less. This specimen also shows a shallow, broad groove at the cardinal angles (Figs. 1 and 2).

A slight groove is also developed at the cardinal angles of a

specimen of *Rhynchotrema capax* (Conrad), No. 142, and of *Atrypa spinosa* Hall, No. 499 (Figs. 8 and 3). In these specimens, however, the groove does not extend to the anterior portion of the shell as it does in some.

3. *Rotation of the Umbos toward Each Other.—This results in greater gibbosity of the shell.*

As shown above, the anterior growth of the valves in old age

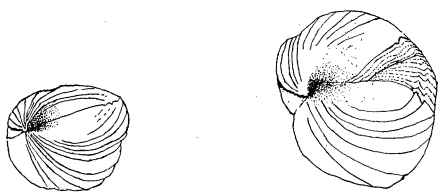

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FIG. 7.— *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. A mature form.

FIG. 8.— A large senile individual of *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. Senility is shown in the lamellose growth lines and in the extreme gibbosity. No. 142, Harvard.

is at a more or less abrupt angle to the previous growth. This gerontic growth thus tends to push the edges of the ephebic shell farther and farther apart, and causes the valves to rotate outward on the axis of the hinge line. This rotation brings the umbos closer and closer together until often the beak of the brachial

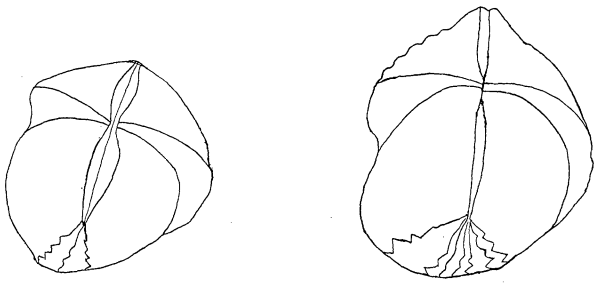

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FIG. 9.— A fully mature form showing in the pronounced growth varices the beginning of senility. *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. No. 1910, M. I. T.

FIG. 10.— An advanced gerontic form of *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. Old age is especially shown here in the strongly lamellose growth lines and in the closely approximated umbos. No. 1911, M. I. T.

valve encroaches on the delthyrium of the pedicle valve to such an extent as to block the original pedicle opening entirely (Figs.

8 and 10). As long as the pedicle remains active it will resorb the umbo of the pedicle valve as fast as the brachial umbo encroaches upon it, thus keeping a passage open for itself (Fig. 11). From this rotation of the valves there results a lengthening of the dorso-ventral axis of the shell. This gives it a gibbous appearance which is seen even in forms that are in maturity flat and thin, as *Rafinesquina alternata*. This great increase in thickness is shown in Figs. 3, 5, and 6, and also in the following measurements:—

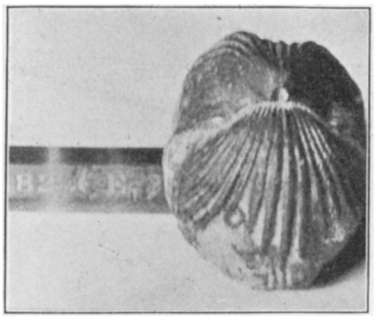

FIG. 11.— *Rhynchotrema capax* (Conrad). Hudson River group of Cincinnati, Ohio. A gerontic individual which has through resorption of the umbo, kept its pedicle passage open *pari passu* with the rotation of the umbos toward each other. No. 1156, Harvard.

Rafinesquina alternata (Figs. 12 and 13). Adult, No. 1912, M. I. T. Length, 32 mm.; breadth, 41 mm.; thickness, 3.5 mm. Old age, No. 128. Length, 39 mm.; breadth, 51 mm.; thickness, 11 mm.

Rhynchotrema capax (Figs. 7 and 8). Adult, No. 1913, M. I. T. Length, 22 mm.; breadth, 21 mm.; thickness, 26 mm.

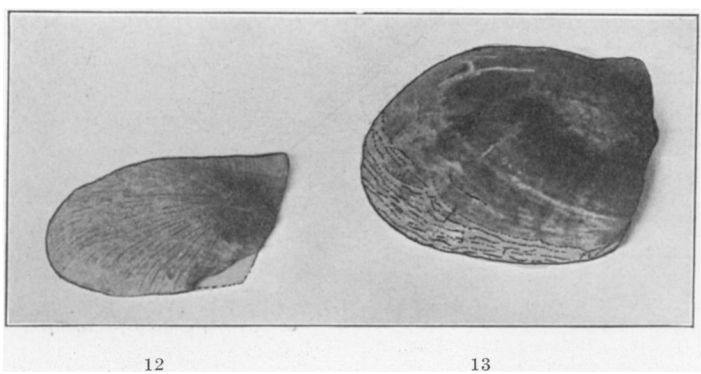

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FIG. 12.— Mature individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio.

FIG. 13.— A large gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, indicating senility in the lamellosity of the concentric growth lines, in the changed angle of curvature, and in the greater gibbosity of the shell. No. 128, Harvard.

4. *Flattening-out of Plications.*—In old age the plications (ribs) tend to flatten out and disappear. Their presence is usually indicated on the gerontic portion of the shell by zigzag lines of growth, though the surface of the shell is at this area smooth. This is seen in *Rhynchotrema capax, Platystrophia lynx, Tropidoleptus carinatus,* Spirifers, etc., and holds true in all specimens examined (see p. 117).

Examples: in *Rhynchotrema capax,* No. 142, from Cincinnati, Ohio, the pedicle valve has during maturity 15 ribs; during metagerontism it has 11, and at the last growth before the death of the animal there are none, although zigzag growth lines represent them. The brachial valve has during maturity 14 ribs; during metagerontism, 10, with none at the death of the animal.

In *Spirifer oweni,* No. 57, from the Hamilton of Clark Co., Indiana, the ribs become broader and lower until in extreme old age they, as well as the zigzag growth lines at the edge of the shell, have almost entirely disappeared even at the anterior portion of the shell (see p. 117 for further discussion).

The ribs disappear earlier and more completely from the brachial than from the pedicle valve. This was noticed especially in *Terebratella plicata* Say, *Tropidoleptus carinatus* (Conrad), *Meekella striatocostata* (Cox), *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, and *Rhynchotrema capax* (Conrad). This character is often only faintly marked; its presence is first noted at the cardinal angles. Raymond (:04, p. 128), also notes the more nearly complete obliteration of the plications on the brachial valve in *Tropidoleptus carinatus.*

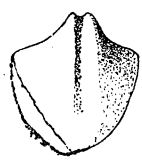


FIG. 14.—A gerontic individual of *Ambocœlia umbonata* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York, showing the disappearance of the median sinus.

5. *Disappearance of Median Sinus and Fold.*—The median sinus and fold tend to flatten out and disappear in a few observed species.

Examples: in *Ambocœlia umbonata* (Conrad) (Fig. 14), the median sinus disappears in old age. In *Bilobites varicus* (Conrad) there is also a tendency to obliterate the marginal sinus. This is shown in a series of shells, No. 4, from the Lower Helderberg of Clarksville, Albany Co., New York (Fig. 15). For further examples see also Beecher (:01, p. 403).

In some species the median sinus appears to become more accentuated with age. For example, *Athyris spiriferoides* shows well this accentuation of the sinus with hardly any corresponding development of the median fold, while in *Cœlospira grabaui* Shimer, both sinus and fold are developed (Shimer, :04, p. 253).

FIG. 15.—Series showing gradual obliteration of the sinus from maturity to old age. *Bilobites varicus* (Conrad) from the Lower Helderberg of Clarksberg, New York. No. 4, Harvard.

6. *Enlargement of Cardinal Angles.*—The cardinal angles, that is, the angles made at the cardinal extremities between the hinge line and the sides of the shell, enlarge during senescence.

Examples: a specimen of *Rafinesquina alternata*, No. 128, has just preceding senescence, a cardinal angle of 87°. This increased to 99° during old age (Fig. 13).

A specimen of *Spirifer mucronatus* var. *thedfordense*, No. 405, has at the close of the neanic or *Spirifer mucronatus* stage (Shimer and, Grabau, :02, p. 171) a cardinal angle of 25°. This angle rapidly increases as seen in Fig. 16, through the ephebic and gerontic stages until it measures 60° at the death of the animal.

7. *Reduction of Shell Index.*—The shell index, *i. e.*, the breadth divided by the length, becomes smaller with old age (see Cumings, :03, p. 3). In other words the shell becomes proportionally longer in old age than in maturity and in this respect approaches the nepionic condition.

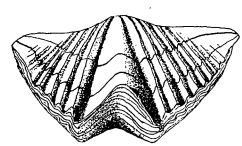


FIG. 16.—A senile form of *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, from the Hamilgroup of Arkona, Ontario. This shows senility in the enlarging cardinal angles and in the piled-up growth lines. No. 405. Harvard.

Examples: a specimen of *Spirifer mucronatus* var. *thedfordense* has during its nepionic stage a shell index of 1.77; during its neanic, 3.57; and during ephebic, 1.90. For further measurements and discussion of the varietal form see Shimer and Grabau (:02, p. 174).

An old specimen of the above species, No. 405a, had during early maturity a width of 34 mm. and a length of 14 mm., giving a shell index of 2.43. In old age the width was 33 mm., the length 18 mm., and shell index 1.83.

Rhynchotrema capax, No. 142, had in maturity a width of 18 mm., a length of 17 mm., giving a shell index of 1.06. In old age the width was 20 mm., the length 23 mm., and shell index 0.87 mm.

In *Rafinesquina alternata*, No. 128, the mature shell measured 42 mm. in width, 30 mm. in length, and the shell index was 1.40; the senile shell was 51 mm. wide by 39 mm. long with a shell index of 1.30.

8. *Modification of Pedicle Opening.— a. The pedicle opening may be enlarged during growth.* As the animal increases in size the pedicle normally increases in diameter if it continues attached. The resulting growth of the pedicle may resorb the surrounding shell (the deltidium or deltidial plates and umbo) and thus enlarge its opening. This is especially conspicuous in the Terebratuloids. In some shells resorption is made doubly necessary if the pedicle would continue to exist, for the rotation of the umbos toward each other would otherwise soon cut it off. This condition is seen well in some specimens of *Rhynchotrema capax*.

Examples: a specimen of *Laqueus californicus*, No. 715, is a senile individual as indicated by its lamellose growth lines, abrupt deflection, and groove at the cardinal angles. The umbo shows considerable resorption as do also the deltidial plates (Figs. 1 and 1a).

A senile specimen of *Hebertella occidentalis* Hall, No. 2, has a triangular delthyrium 9 mm. high, 5.5 mm. wide at the hinge line, and 2.5 mm. at the apex of the umbo. The delthyrium, already large in maturity with the deltidium resorbed, has been much enlarged in old age; in addition the umbo of the pedicle valve has been resorbed, destroying much more than the nepionic shell (Fig. 17). This destruction of the umbo may be partially due to breaking as shown by an irregularity at the anterior side, but there is no doubt that most of the opening is due to resorption

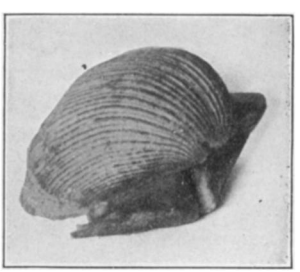


FIG. 17.— A subgerontic individual of *Hebertella occidentalis* Hall from the Hudson River group of Cincinnati, Ohio, showing the pedicle opening much enlarged through resorption of the umbo. No. 2, Harvard.

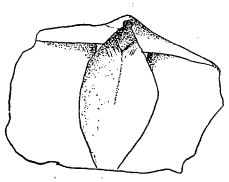
as it has the same general smoothness and evenness of the sides as the delthyrium.

In those forms of *Rhynchotrema capax* which continue attached throughout life, the increasing gibbosity makes necessary, even during late maturity, a resorption of the umbo of the pedicle valve. But this resorption becomes very great in senile specimens, as for example in a specimen, No. 1156, the apex of whose pedicle valve has been resorbed anteriorly at least 1.5 mm. (Fig. 11). The smoothness of this opening and the evenness with which it is prolonged out from the interior of the shell show it to result from true resorption and not from breaking.

b. The pedicle opening may be partially or completely closed. This is accomplished:—

(1) By deposits of calcareous matter in the apex of the valve, sometimes forming a callosity.

Example: in *Stropheodonta demissa* (Conrad), No. 1914, M. I. T., the delthyrium has been completely closed by growths that extend from either side and meet in the middle; these form two



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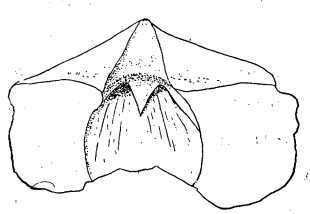

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FIG. 18.— The interior of the pedicle valve of a mature form of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the beginning of the callosity in the pedicle cavity.

FIG. 19.— The interior of a pedicle valve of a gerontic individual of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the accentuation of the callosity. No. 646, Harvard.

convex callosities on the inner or proximal side which meet in the median line. The outside of these growths is smooth and also the cardinal margin is wanting in the denticulations characteristic of the rest of the shell.

A testaceous callosity sometimes forms in the pedicle cavity, and extends across the delthyrium (see also Hall and Clarke, '94a, p. 6). This is seen in *Spirifer acuminatus* (Conrad), *S. granulosus* (Conrad), and *S. audaculus* (Conrad).

Example: in a gerontic pedicle valve of *S. acuminatus*, No. 646, the callosity extends 17 mm. from the apex of the valve to the anterior border, uniting the dental lamellæ and sending off a median portion forward between the posterior extremities of the diductor muscle impressions. In a mature valve of this species there appear only faint indications of this callosity in the apex (Figs. 18 and 19). Hall and Clarke ('94a, p. 921), mention this deposit of calcareous matter in the apex of the valve as a frequent condition in senile Spirifers. They also state that "the tendency to contract the pedicle cavity and deltidium presents its extreme manifestations in the Devonian forms of Stropheodonta, Strophonella and Leptostrophia where it has become almost and sometimes quite obliterated and the entire umbonal area filled with testaceous secretions" (Hall and Clarke, '94a, p. 919).

(2) By the encroachment of the umbo of the brachial valve upon the delthyrium of the pedicle valve, so as partially or completely to cover it. This follows from the rotation of the umbos toward each other in senescence as already described (p. 99). When its original opening is thus covered, the pedicle may keep its passage free by resorption into the umbo of the pedicle valve, as already seen (Figs. 1, 11, 17), or may become atrophied and disappear, leaving the shell unattached.

Examples: in a senile specimen of *Platystrophia lynx*, No. 1911, M. I. T., the umbos are so closely appressed that no pedicle opening can be seen (Fig. 10). An approach to this condition is seen in many senile Spirifers, *Rhynchotrema capax*, etc.

9. *Disappearance of Spines, Nodes, etc.*— In old age the surface tends to become smooth, thus repeating the nepionic surface character. In all forms this is noted first at the angles and later at the anterior portion of the shell. There is slight development of surface ornamentation among the brachiopods beyond the simple plications and median sinus and fold. This lack is especially noticeable when we compare this class with the pelecypods, gastropods, and cephalopods which are often characterized by an excessive development of ribs, spines, nodes, etc. If, in brachiopods, spines or nodes are present in maturity, they gradually become less numerous until in extreme old age they disappear entirely (see also Hyatt, '89, p. 20, and Beecher, :01, p. 94). Examples are noted in Productus, Atrypa, and Ambocœlia.

Productus horridus, No. 600, 43 mm. wide and with a length of 82 mm. following the curve of the pedicle valve, has no spines on the last added 12 mm. of the anterior portion, while the spines had disappeared earlier from the surface at the cardinal angles (see p. 110).

Another specimen of the same species, No. 607, has no spines on the last added 18 mm. This disappearance of spines in old age is also well seen in *Ambocœlia spinosa* and in *Atrypa spinosa*. In *Atrypa nodostriata* the disappearance of nodes from the senile portion of the individual was noted.

10. *Thickening of Valves.*—This may result in the formation of an elevated ridge about the muscular area and in the building of a ridge just inside the margin of the concave valve in concavo-convex forms. Both valves, and especially the pedicle valve, thicken by interior additions. The area of maximum increase usually extends from each side of the muscular impression to the cardinal angles. Sometimes, as for example in *Athyris spiriferoides*, the greatest thickening is at the lateral edges of the valves. The pedicle valve becomes especially thickened over the gential organs as seen in Atrypa, Spirifer, etc.

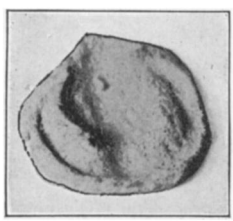

FIG. 20.— The pedicle valve of a gerontic specimen of *Atrypa reticularis* (Linné) from the Lower Helderberg near Catskill, New York. Old age is shown by the greatly thickened and inflected edge of the shell and in the prominent ridge bounding the muscular area. No. 641, Harvard.

Examples: a pedicle valve of *Atrypa reticularis*, No. 641, has a broad, prominent ridge bounding the muscular area laterally and sloping outward to a depression between it and the much thickened and inflected edge of the shell; it disappears entirely anteriorly (Fig. 20).

A pedicle valve of *Spirifer acuminatus*, No. 646, shows a greatly depressed muscular area due to the great thickening of the posterior portion of the valve on each side of it, which slopes gradually to the lateral margins of the valve (Fig. 19).

In *Platystrophia lynx*, No. 3, the pedicle valve is thickened very much at the sides of and anterior to the muscular area (see also Cumings, :03, p. 28).

In the above cases, as well as in all observed, the greatest thickening in the interior of the valve occurs in the region of the principal trunks of the vascular sinuses, and it is in these main trunks that in modern brachiopods the genital organs occur (for further discussion see p. 117). In most concavo-convex and resupinate shells the concave valve bears just inside its margin and posterior to where the convex valve fits over it, a swollen and strongly papil-

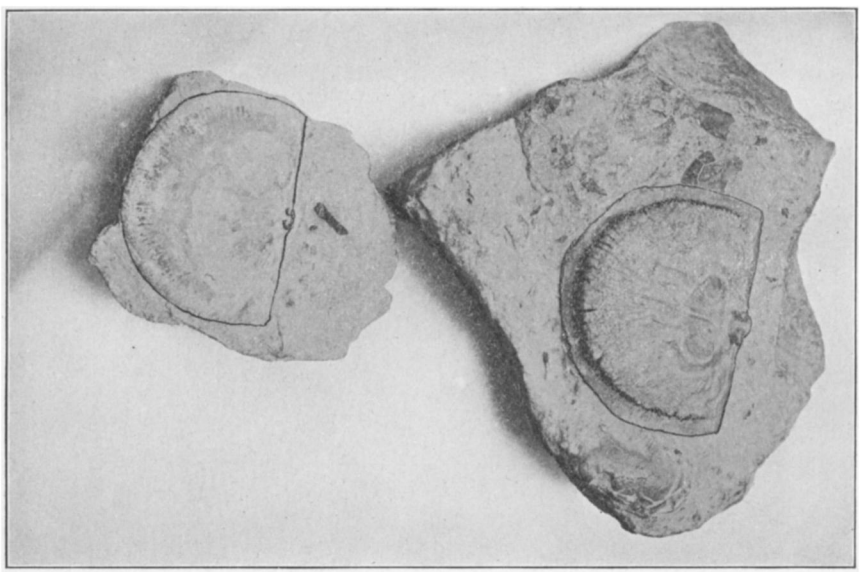

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FIG. 21.— A mature brachial valve of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati. Ohio. No. 1, Harvard.

FIG. 22.— The brachial valve of a gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, showing the vascular tumid ridge and its abrupt descent to the edge of the valve. Harvard collection.

lose ridge which extends from the cardinal angles to the anterior portion of the shell. In the brachial valve of *Rafinesquina alternata* the ridge has a very irregular surface and descends abruptly to the narrow margin of the valve. This makes the interior of the valve quite flat while the outside is concave (Fig. 22). This submarginal thickening was also noted in *Tropidoleptus carinatus* (Conrad), *Strophomena rugosa* Blainville, *Plectambonites sericeus* (Sowerby), *Chonetes granulifera* Owen, *Stropheodonta magniventra*

Hall, and *S. concava* Hall. Sometimes the papillæ are so well developed that they are spine-like. This was most conspicuous in *Stropheodonta magniventra*, No. 1165, and in *S. concava*, No. 1099, M. I. T.

In the majority of brachiopods the muscular area of the pedicle valve becomes in gerontic individuals depressed below the general interior level of the shell through the thickening of the shell about it, and thus frequently leaves this area translucent in its thinness while the remainder of the shell is very thick. The area is often strongly marked off from the rest of the valve by an elevated ridge at times high and well defined, surrounding it. This ridge is

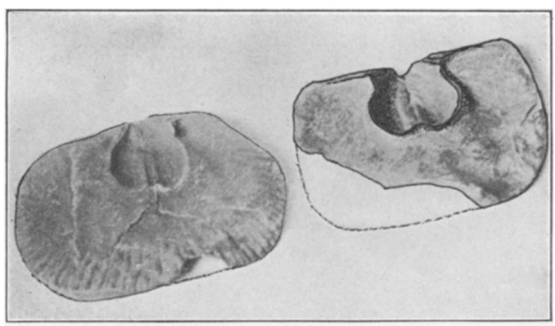

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FIG. 23.— The pedicle valve of a mature specimen of *Hebertella occidentalis* Hall.
FIG. 24.— The pedicle valve of a gerontic individual of *Hebertella occidentalis* Hall, showing the high ridge defining the muscular area.

conspicuous in *Rafinesquina alternata*, *Leptæna rhomboidalis*, *Hebertella occidentalis* (Fig. 24), *Eatonia peculiaris*, and *Hipparionyx proximus*, in all of which the muscular area is strongly marked off from the rest of the shell. In *Spirifer acuminatus* (Fig. 19) the ridge surrounding the muscular area is merged with the general thickening of the shell. We have not been able to examine any senile forms in which the dental lamellæ of the pedicle valve are strongly developed and form a spondylium, as for example in Pentamerus, Gypidula, etc. In these the muscular area is thus raised instead of retaining its youthful position. This thickening of the valves may in a few individuals result in the lessening of the total capacity of the body chamber. Usually,

however, the internal thickening is more than offset by the growth of the margins of the valves toward each other; for even a slight marginal growth means a large increase in the cubic capacity of the shell.

Descriptions of a few Species

The following species were chosen for description of senescence because there were gerontic specimens of them in the collections studied and also because they are common. Similar old age characters were, however, noted upon all forms which showed any approach to gerontism. When one specimen is described, this is merely taken as a type but the characters hold true for all the specimens of that species examined.

Rafinesquina alternata (Emmons).—A large specimen, No. 128, from the Hudson River group of Cincinnati, Ohio, was 30 mm. long when it first showed signs of old age in the appearance of lamellosity and in the changed angle of curvature; this change is much more noticeable on the pedicle than on the brachial valve. The shell also increases in thickness from 3.5 mm. in a normal mature specimen to 11 mm. in this gerontic individual. In old-age specimens of this species the pedicle opening is usually entirely closed and if it exists, is much too small to admit the passage of a pedicle large enough to support a shell of such a size (on this point see also Hall and Clarke, '92, p. 141). This condition is not, however, due wholly to senility but existed during maturity.

The interior of the brachial valve has, extending from the cardinal angles around the margin of the valve anteriorly, a tumid ridge with a very irregular surface. This descends abruptly to the edge of the valve. For comparison of mature and gerontic forms see Figs. 21 and 22.

Strophomena rugosa Blainville (*Streptorhynchus planumbonus* Hall).—A pedicle (concave) valve, No. 582, of this species bears just inside its edge a tumid ridge with a considerable vascular surface, which is not developed to such an extent as in the concave (brachial) valve of *Rafinesquina alternata*. This fact is interesting as the ridge is developed in opposite valves in the two species. The muscular area remains translucent while the rest of the valve

becomes much thickened and more or less grooved by vascular markings. Both valves of this species bear lamellose growth lines. There is also a greater lamellosity in the latest built portion of the deltidium and chilidium.

Productus horridus Sowerby.— No. 600 from the Lower Zechstein of Gera, Thuringia, is not very senile. Old age, however, is indicated by the greater concavity of the brachial valve and by the absence of spines from the last added 12 mm. of the anterior portion. They had disappeared before this from the cardinal angles, showing thus the progressive advance of senility from the cardinal angles to the anterior portion. This order of disappearance is just what we should expect from their order of initiation, appearing as they do at the cardinal angles before they develop on the main portion of the shell.

Platystrophia lynx (Eichwald).— A gerontic individual of this species from the Hudson River group of Cincinnati, Ohio, No. 1911, M. I. T., attained a length of 31 mm. before it began to show evidence of old age in any marked degree; after this point it added a length of 13 mm. to each valve. The senescent characters noted here are: lamellosity of growth lines, flattening of the ribs, and formation of a groove at the cardinal angles. Through the change in the angle of curvature and the consequent growing toward each other of the two valves, the entire shell becomes very gibbous. The accentuation of these characters in increasing old age may be seen by comparing Figs. 9 and 10. The cardinal angle measures 78° at the close of the ephebic stage and 94° in the gerontic. Similar observations are given by Cumings (:03, p. 12).

A pedicle valve of this species, No. 3, from the Hudson River group of Cincinnati, Ohio, shows a very pronounced thickening on each side of and anterior to the muscular area. This area thus appears to be very much depressed, with high, perpendicular bounding walls. The development and relationship of this species are very thoroughly discussed and illustrated by Cumings (:03).

Rhynchotrema capax (Conrad).— A specimen of this species, No. 142, from the Hudson River group of Cincinnati, Ohio, after reaching maturity when it had a length of 15 mm., became lamellose at the cardinal angles and the ribs began to flatten out, while the angle of curvature in each valve became relatively greater.

It then lengthened the pedicle valve 8 mm. on the curve of the shell, during ana- and metagerontism. At this point the growth lines become still more lamellose, more of the ribs flatten out, and a sudden increase in the angle of curvature takes place. From this point it added 7 mm. to each valve. There is shown especially on the median sinus and folds of this latest added portion a groove in the center of each rib on account of the changed plane of growth. A shallow groove is formed at the junction of the valves. This is greater at the cardinal angles since it is there first formed and proceeds progressively anteriorly. This groove is due in the anterior portion to the last added two or three growth lines only. The specimen has the pedicle opening entirely filled by the umbo of the brachial valve. Another specimen, however, No. 1156, as large as the preceding and representing a similarly advanced stage of senescence, has a very large pedicle opening. Mature and gerontic forms are shown in Figs. 7 and 8.

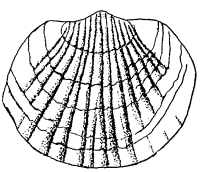

FIG. 25.—A senile individual of *Tropidoleptus carinatus* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York. Old age is indicated in the enlargement of the cardinal angles, reduction of shell index, and in the flattening-out of the ribs. These last always disappear progressively from the cardinal angles to the front of the shell. No. 1915, M. I. T.

Terebratula harlani Morton.— In this species old age is shown in the lamellose concentric growth lines, the change in the angle of curvature, the groove at the cardinal angles, the larger cardinal angle, and the resorption of the umbo and deltidial plates. Exactly similar characters are shown in *T. perovalis* Sowerby.

Tropidoleptus carinatus (Conrad).— In an old-age specimen of this species, No. 1915, M. I. T., the ribs are flattened out on the gerontic portion and the growth lines are lamellose, irregular, and more or less piled up. These senile characters appear progressively from the cardinal angle to the front of the shell (Fig. 25). The cardinal angle enlarges and the shell index grows smaller. The ribs flatten out on the brachial valve before they do on the pedicle valve. In other specimens the submarginal ridge of the concave (brachial) valve, so characteristic of *Rafinesquina alternata*, also occurs, though in a less marked degree. Raymond (:04, pp. 126–131) discusses this species fully.

Laqueus californicus Koch.—A specimen of this recent species, from Catalina Island, California, No. 715, shows old age in the lamellose growth lines, the change in the angle of curvature, and the formation of a groove at the cardinal angles, and in the larger cardinal angles (Figs. 1 and 2). These characters also appear in *L. rubellus* Sowerby, etc.

Atrypa spinosa Hall.—In a specimen from the Hamilton of Eighteen Mile Creek, New York, No. 499, old age is first indicated after a growth of 27 mm. by the sudden crowding together of the growth lines and by the change in the angle of curvature. After this the anterior growth through the change in curvature adds about 5 mm. to the thickness of the shell and 4 mm. to its length measured along the antero-posterior axis. This gives the shell a very gibbous appearance. Senility is first expressed at the cardinal angles as seen in the development there first of the greater lamellosity of the growth lines, the change in the angle of curvature, and the formation of a groove which does not extend far anteriorly. The thickness of the comparatively flat pedicle valve is much greater than that of the brachial. For comparison of the senile characters of this specimen with an adult form, see Figs. 3 and 4. A pedicle valve, No. 641, shows the separation of the muscular area from the rest of the valve by a thick, prominent ridge which is especially developed at its sides, *i. e.*, over the genital organs (Fig. 20). The thickened lateral edges of this form a prominent inflected edge.

Spirifer mucronatus var. *thedfordense* Shimer and Grabau.—A specimen of this species, No. 405, from the Hamilton group of Arkona, Ontario (Fig. 16), shows old age in an increase of the lamellosity of the concentric growth lines, the fading-out of the ribs, the change in the angle of curvature, and the development of a groove cardinally at the junction of the two valves. These characters hold true in all senile specimens of this genus examined. In *S. acuminatus* the greatest thickening of the valves is on each side of the muscular area. This character appears to hold true in all species. In some species (*e. g.*, *euryteines*, *acuminatus*, *oweni*, etc.) a conspicuous thickening (callosity) occurs also posterior to the muscular area in the pedicle valve, thus separating it widely from the apex of the valve (Fig. 19).

Nucleospira ventricosa Hall.— Senility in this very small, Lower Helderberg species is shown by a conspicuous roughness or lamellosity of the concentric growth lines in the otherwise smooth shell, a change in the angle of curvature, and the formation of a reëntrant groove at the cardinal angles, the point where senility is first indicated. No shell sufficiently senile to have developed a groove in the anterior portion was observed.

Athyris spiriferoides (Eaton).— One specimen from the Hamilton of Eighteen Mile Creek, New York, No. 498, was 22 mm. long and 26 mm. wide when senescent characters first appeared. After that it grew 10 mm. anteriorly measured on the curve of the shell. This growth increased the antero-posterior axis only 6 mm. The maximum width of the pedicle valve was increased only 2 mm. though the total amount added to the width in old age measured over the curve of the valves, was 11 mm. The rest of the growth both anterior and lateral merely added to the thickness of the shell. In this shell old age is expressed by the lamellosity of the growth lines and the change in the angle of curvature. This latter character is more especially noticed at the sides of the pedicle valve as this valve piled up growth lines here to a thickness of 4.5 mm. The lateral edges of the brachial valve thickened less. A groove was formed at the junction of the valves. The cardinal angle enlarged from 100° in the mature shell to 125° in parageröntism (Fig. 6). This specimen shows the normal progression of old age characters from the cardinal angles to the anterior border, in the first appearance there of the lamellose growth lines and of the groove. This groove at the death of the animal had advanced only halfway to the anterior border of the shell. A separate pedicle valve, No. 635, shows the maximum thickening from each side of the muscular impression to the cardinal angles, with the greatest thickening at the edge of the valve. Figs. 5 and 6 show for comparison a mature and a gerontic individual.

Conclusions.

Minot ('91, p. 151) says very suggestively: "I think it is now conclusively established that there is in guinea pigs a progressive

loss in the power of growth, beginning almost immediately after birth." This same decrease is very realistically shown in the little gastropod, *Litorina littorea*, so abundant on our Atlantic coast. This shell, in the vicinity of Boston, is very quickly attacked by an alga which discolors and erodes it. So if a series of the shells from small to large is collected at mid- or late summer before the new growth has become corroded by the algæ, the amount of that year's growth is very distinctly shown. Such a series shows that, while on the small specimens the year's growth was more than two complete whorls, in older specimens it became progressively less until in some of the mature ones it was but 3.5 mm. Finally on the older shells growth was extremely reduced, being on one shell only 0.75 mm. For these facts concerning Litorina we are indebted to Professor R. T. Jackson whose series of these shells collected from Manchester, Mass., shows the above facts. The series is now on exhibition at the Boston Society of Natural History.

This relative decrease in growth is also shown in the crowding of the septa in old-age cephalopods. Among pelecypods and brachiopods the relative decrease in the amount added to the shell is indicated in the more crowded condition of the later added growth lines. For example, a specimen of *Atrypa reticularis*, No. 641, shows 12 growth lines on the gerontic portion which give a thickness of 5 mm. while the preceding growth, about 22 mm. long, has also only 12. Yet if the growth lines were added at regular time intervals the gerontic stage represented as long a period as that from embryonic through ephebic.

That the more prominent growth lines may define the shell growth for definite periods of time is indicated in the following examples. Buxbaum showed that *Anodonta cellensis*, one of the Unionidæ, had two strongly marked concentric lines and hence three sets of more faintly marked areas, and this shell was known to be three years old (Latter :04, p. 163).

The common oyster commercially marketed is about four years old when gathered. Blue Points, which are smaller, are three years old. This age is broadly indicated on the shells by the stronger growth lines. On the Litorina cited above, the new growth is usually bounded posteriorly by a prominent growth line.

While thus the increase in the size of the animal becomes less and less for each succeeding growth period, a time is reached, varying with each individual, when another factor enters and actual decrease or shrinkage begins. The tendency of the soft parts of animals to contract in old age is familiar to us. (See Hyatt, '96, p. 15; Quain, :03, p. 1478). Through this tendency can be explained many alterations in the hard parts which are otherwise difficult of explanation.

The soft parts and especially the mantle of brachiopods, as well as of molluscs, are so closely related to the shell (Morse, :02,

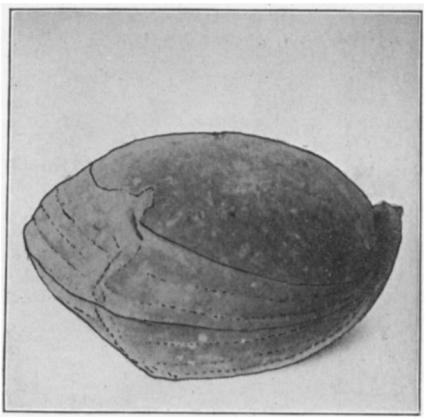

FIG. 26.— Shell showing gerontic effects produced by injury. *Laqueus californicus* Koch from Catalina Island, California. No. 738, Harvard.

p. 321) that the least change in the former is expressed in the latter. For example, a specimen of *Laqueus californicus* Koch, No. 738, had the anterior portion of the mantle injured. The scars occur in the same relative position on each valve, and the mantle edge left a groove on the shell, indicating the scar (Fig. 26). Before the animal was injured the surface of the shell was very smooth, showing no signs whatever of declining strength, but as soon as the injury occurred a lessened vitality is very noticeable in the change in the angle of curvature and in the lamellose growth lines, simulating senescence.

A change in the angle of curvature of the shell shows that the soft parts of the animal have ceased to grow as fast as formerly. When, however, we consider such gerontic individuals as *Athyris*

spiriferoides, No. 498 (Fig. 6), and *Atrypa spinosa*, No. 499 (Fig. 3), as described above, it is evident that the growth of the soft parts must have practically ceased, while their secreting activities were continued, but were now almost entirely directed toward thickening the shell (see also Beecher, :01, p. 91).

The formation of a groove at the junction of the valves means further, not only that the growth of the mantle has ceased, but that it is in fact growing smaller, in other words is shrinking. As noted above in the description of *Athyris spiriferoides*, etc., the width of the shell on the right and left axis is less during parageron-tism than it is during the earlier anagerontic stage. This tendency of the soft parts of the animal to shrink and to express this shrink-age in the hard parts is also well exhibited among pelecypods and cephalopods.

The lamellosity of the growth lines in such types as Athyris,

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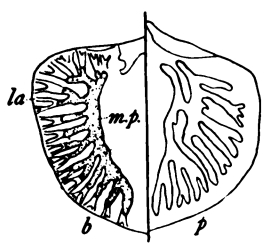

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FIG. 27.— The pedicle valve of a senile individual of *Atrypa reticularis* (Linné) from the Lower Helderberg of Catskill, New York. The prominent ridge surrounding the muscular area occurs beneath the main vascular sinus. No. 641. Harvard.

FIG. 28.— The pedicle valve of *Atrypa reticularis* (Linné) showing the muscular (*m*) and vascular impressions with the ovarian markings (*o*) within the main vascular sinus of the latter. (After Zittel.)

FIG. 29.— Brachial and pedicle half of pallium of the recent *Terebratulina coreanica* with the main pallial sinus and lacunæ filled with eggs. *b*, brachial valve; *p*, pedicle valve; *la*, lacuna; *m. p.*, main pallial sinus (after Morse).

Atrypa, etc., is caused by the relatively decreasing extent of the successive lamellæ of shell growth built in old age. This as resultant brings about a change in the angle of curvature which in extreme cases causes even a resultant angle of less than 90°.

The thickening of the shell on the interior often takes place very irregularly, and leaves the surface strongly papillose. This is well seen in the Spirifers, Stropheodontas, etc. In some Strophe-

odontas, as noted above (section 10), these papillose protuberances become almost spine-like.

The principal thickening in at least many brachiopods occurs over the main trunks of the vascular sinuses (compare Figs. 27, 28, 29; see also Fig. 22). It is a significant fact that in these are located the genitalia (Hancock, '59, p. 817). If a greater contraction took place there it is just in line with what we know occurs in higher animals (Quaïn, :03, p. 1478). It is usually held that "no gerontic limit is known to the reproductive time in the lower animals" (Hyatt, '97, p. 220). As there is doubtless in most shells an increasing amount of space unoccupied by the soft portion of the animal as it increases in age, it is not necessary to postulate a great shrinkage of the soft tissues to account for the thickening of the shell. Yet the fact remains that in many species the principal thickening is over the main trunks of the vascular sinuses, just where the genitalia occur in modern species and where very probably they were located in fossil ones.

The greater reduction of the lateral growth of the mantle over that of anterior growth in brachiopods is seen in the fact that in old age the shell is proportionally longer than in maturity. The result of these old-age processes appears first at the cardinal angles where the loss of lateral growth to compensate for the shrinkage, causes the flattening-out of the mantle folds (see also Williams, '95, p. 309). The reduction of the radial ribs proceeds progressively from the cardinal angles to the anterior border of the shell and hence it is on the sinus and fold that we find the ribs persisting strongest.

In those cases where the ribs flatten out entirely their continuance is indicated by zigzag lines of growth on the smooth surface of the gerontic portion of the shell. These show that the mantle, after flattening out on one plane, still retained the scalloped border on another. This scalloped edge (as seen for example in *Rhynchotrema capax*) resulted from the faster growing of parts of the mantle over others. As the mantle curved, the parts which formed the summits of the ribs fell behind those which formed the depressions. In other words the portions in the depressions grew faster. This difference in the rate of growth may be seen by following two ribs and their included sinus from the umbo to the front of

the shell, plotting the angles and lengths of the successive growth lines in crossing them (Fig. 30). Thus when the shell surface becomes smooth in old age the zigzag lines of growth where present represent the successive positions of the mantle border. It is as if the plications had been merely transferred from the vertical to the horizontal plane, as the actual mantle is probably scalloped to the same degree in both cases and the absence of ribs results simply from the changed angle of curvature of the shell. Often, however, there is a tendency of the mantle edge to fill out the scallops and to present a smooth edge. A beginning in this direction can be seen at the cardinal angles of many plicate individuals. Examples of this are noted in very old specimens of *Spirifer oweni*, *Rhynchotrema capax*, etc.

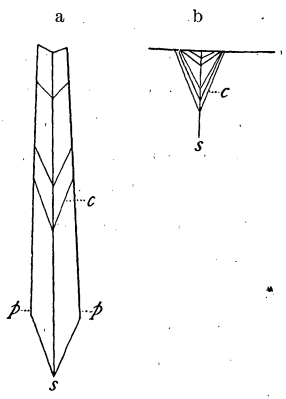

FIG. 30.— Diagrams showing the slower growth of the plications when compared with the furrow between. *a*, enlargement of a furrow and its bounding plications with a few concentric growth lines; *b*, the growth lines of the preceding superimposed on one another, showing graphically the greater growth in the furrow; *p*, plication; *s*, sinus or furrow; *c*, concentric growth lines. These figures were plotted from the median sinus of a specimen of *Rhynchoterma capax*, No. 142, Harvard. × 2½.

The continued anterior growth after the practical cessation of lateral growth causes the cardinal angles to increase in size and causes also the shell index to decrease (see sections 6 and 7). This is a taking-on again of the large cardinal angles and small index of the nepionic stage.

Not only is there repetition of youthful characters in the outline of the shell but there is also a similar repetition in the loss of ornamentation, for the nepionic shell is smooth. An old man with his bald head, curved back, toothless gums, and size smaller than during maturity, resembles the child. Though in these and in many other respects the resemblance is very striking yet in the child the form is the result of positive, developing factors; in the man it is negative, degradational (see also Hyatt, '97, p. 218). So among brachiopods the enlargement of the cardinal angles, reduction of shell index, and the obliteration of ribs, spines, nodes, etc., are in a certain sense a return to the features seen in the nepionic

stage, yet it is a resemblance due to loss of characters. It is thus essentially different from the developing of the similar characters in youth. The characters usually disappear from the shell in the inverse order of their initiation (see also Hyatt, '94, p. 20, and Beecher, : 01, p. 269).

As seen above, senility is first shown at the cardinal angles and from there it takes place progressively to the anterior portion of the shell. Hence it is at the cardinal angles that we look for the first expression of old age,— as a change in the angle of curvature, lamellose growth lines, flattening of ribs, and development of a groove at the junction of the valves. Very rarely are individuals found sufficiently old to have expressed on the anterior portion of the shell all of the above senile characters.

When these characters do not appear simultaneously on the shell they appear in a definite order, *viz.*, (1) flattening of ribs, (2) lamellose development of concentric growth lines, (3) change in the angle of curvature, (4) formation of a groove at the junction of the valves, (5) flattening of sinus and fold. This is the usual order, though at the cardinal angles they frequently occur at approximately the same growth line.

Originating thus at the cardinal angles, these gerontic features are pushed farther and farther forward until in parageronticism they are present on the most anterior portion of the shell.

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